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A frog's eye view: Foundational revelations and future promises

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ABSTRACT

From the mid-19th century until the 1980's, frogs and toads provided important research models for many fundamental questions in visual neuroscience. In the present century, they have been largely neglected. Yet they are animals with highly developed vision, a complex retina built on the basic vertebrate plan, an accessible brain, and an experimentally useful behavioural repertoire. They also offer a rich diversity of species and life histories on a reasonably restricted physiological and evolutionary background. We suggest that important insights may be gained from revisiting classical questions in anurans with state-of-the-art methods. At the input to the system, this especially concerns the molecular evolution of visual pigments and photoreceptors, at the output, the relation between retinal signals, brain processing and behavioural decision-making.

1. Introduction

The frog might be surprised to find itself in the company of" non-model species", but that is the present status of this traditional tetrapod model (*frog* here used generically as *anuran*). In a 1026- page volume titled" Frog Neurobiology" published in 1976, the editors Rodolfo Llinás and Wolfgang Precht note that" studies of nerve conduction, neuromuscular transmission, neuronal integration, sense organs, development and locomotion have been developed with great detail in the frog and in conjunction provide the most complete holistic description of any nervous system" [1]. Attesting to the frog's importance in visual neuroscience, no less than 200 pages are devoted to vision. In molecular and integrative biosciences, however, "model" has come to refer primarily to human relevance, and the frog is not a mammal, still less a primate.

Although supplanted in the biomedical mainstream by the much less visually-oriented mouse, frogs and toads have many properties that make them continuously attractive and interesting for vision research. First, the viability of the eye, retina and retinal cells *ex vivo* at a wide range of temperatures is an enduring practical advantage. Second, their development as free-living, seeing morphs functionally straddles the vertebrates' evolutionary transition from aquatic to terrestrial life, with a comprehensive metamorphosis that includes profound changes in the visual system [2,3].

Third, their retina, whilst representing the basic vertebrate architecture, is unusually sophisticated as an information-processing "accessible part of the brain", which inspired the grand idea of feature-extracting neural computations [4,5]. Fourth, they offer several experimentally useful, innate visually-guided behaviours, and can also be trained [6]. Fifth, and maybe most importantly today, they show a rich spectrum of ecological diversification on a background of shared evolutionary constraints [7].

Many fundamental mechanisms of vertebrate vision were first unravelled in frogs or other amphibians. On that solid foundation they offer unique possibilities for comparative studies that provide a deeper understanding of options, mechanisms and limitations relevant to all vertebrates. Even in human-oriented research, the question" *why this way and not differently?"* should be asked more often beside the usual scientific questions" *what?"* and" *how?"*.

In this review, we especially focus on two fields where frogs and toads have played a significant part in laying the foundations of visual neuroscience, and suggest future directions where they may continue to do so. One concerns visual pigments and photoreceptors, the other the relation between information encoding by retinal ganglion cells and behaviour. More broadly, we ask what can be learned from the basic functional parameters of anuran vision (sensitivity and spatio-temporal as well as chromatic resolution) viewed under a naturalist perspective, *i.e.*, related to habitats, diurnal rhythms, life histories and evolution.

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2. Visual pigments and photoreceptors

2.1. Landmark discoveries

In 1851 Heinrich Müller wrote:" The rods of frogs look somewhat reddish when lying on top of one another to a certain thickness, and an isolated rod may look alternately colourless or coloured depending on whether it is viewed from the side or the end" [8]. This is the first recorded observation of the rod pigment later called rhodopsin. A quarter century later, Franz Boll made the observation that the colour of the red rod mosaic of the frog's retina is changed and finally lost (bleached) under illumination [9]. The truly novel inference was that neuronal excitation could be initiated by a photochemical reaction. Willy Kühne [10] confirmed the results in extensive studies of the substance that Boll had called *Sehroth* (visual red) and Kühne called *Sehpurpur* (visual purple) in intact rods as well as pigment extracts. He remarked on the" happy agreement" between visual-purple regeneration and the galvanic current (*i.e.* electroretinogram, ERG) first recorded by Frithiof Holmgren [11] as regards their persistence for similar durations in frog eyes after the death of the animal. Funnily enough, this elicited a vigorous rebuttal from Holmgren, who reported that frog eyes could still produce electrical light responses when all pigment (so he thought) had been bleached. "From this we conclude that the visual purple is of no essential significance for vision" [12].

While many different photochemical mechanisms could have been theoretically possible, George Wald unravelled the ubiquitous Vitamin-A basis of vision [13,14], with the frog in a central role. In his Nobel lecture [15], Wald describes his postdoc "Wanderjahr" in Germany in the early 1930's: "Then I went to Meyerhof in Heidelberg to do something else, but with a shipment of frogs that had gone astray, I found retinene, an intermediate in the bleaching of rhodopsin". In the following years, fundamental work on the interplay of light and heat in bleaching "visual purple" was done on solutions of frog rhodopsin [16–18]. An important field-opening advantage of using frogs was that light-evoked electrical signals could be studied and combined with visual photochemistry in photoreceptors from the same retina. In 1937, Granit's frog ERG [19] together with Lythgoe's spectrophotometric measurements [16] enabled the first comparison of sensitivity spectra of rod light responses and rhodopsin absorbance spectra in one and the same species (*Rana esculenta,* now *Pelophylax lessonae* × *P. ridibundus*).

The suction pipette technique for recording the light-sensitive current of single rods [20] brought anuran rods to the forefront again. The thick, long and resilient rods of the cane toad (*Rhinella marina*, formerly *Bufo marinus*) were the preparation of choice for much of the early work. Gordon Fain had shown that only 10–15 % of the voltage signal recorded by intracellular electrodes in a cane toad rod *in situ* comes from photoisomerizations occurring in that rod [21], but the new technique enabled close study of phototransduction relatively free from effects of photoreceptor coupling and voltage-sensitive channels. It triggered an avalanche of electrophysiological experiments that were instrumental in clarifying the main features of vertebrate phototransduction. Although this involved studying a diversity of species, anurans (and also urodeles) remained important, sometimes maybe thanks to easy access to the animals in nature around the lab. Thus the rods of local Russian frogs (*Rana temporaria*) served the pioneering patch-clamp work of Fesenko et al. (1985) [22] that nailed cGMP as the internal transmitter directly controlling the light-sensitive conductance of vertebrate photoreceptors. The fine-tuning and validation of what has become the standard template for visual-pigment absorbance spectra, that of Victor Govardovskii and colleagues [23], relied importantly on the high accuracy of spectral data obtained from big anuran rods by microspectrophotometry and suction-pipette recording.

2.2. Spectral and thermal properties of visual pigments

The suction-pipette technique enabled study of thermal properties of the rhodopsin molecule thanks to the high amplification by phototransduction in a dark-adapted rod, making a single-molecule activation visible as a discrete "bump" in the circulating current. As first shown in the cane toad, photoactivations and spontaneous thermal activations of visual pigment produce indistinguishable quantal bumps, and measuring the rate of such bumps in rods in darkness ("dark events") allows estimation of the frequency of thermal activations [24]. Randomly occurring thermal activations constitute a light-identical (and therefore inexorable) noise that must in principle set an ultimate limit to absolute sensitivity and dim-light performance in any species. In the toad *Bufo bufo*, the limitation has been traced from rods to behaviour [25–27] (see 3.4. below).

Based on suction-pipette recordings of dark noise in a large number of rod and cone types from different species with different spectral sensitivities, it is now a well-established fact that the two main functional variables of visual pigments, spectral absorbance and thermal stability, are strongly correlated. Long-wavelength-sensitive pigments, having the capacity to be activated by low-energy photons, are "noisy" (have high probabilities of purely thermal activation) compared with short-wavelength-sensitive pigments, which require higher photon energies for activation [28,29]. Thus, for example, red-shifting a pigment for optimal signal/noise performance in long-wavelength-dominated light environments entails a trade-off between the advantage of increasing photon catch and the disadvantage of increasing noise. This can explain why rod pigments tend to be systematically blue- shifted from the spectral position that would provide the highest quantum catch [30,31]. The strong evidence for spectral-thermal coupling has, on the other hand, come to obscure the complementary question: how far can thermal stability still be modified independently of spectral absorbance? Across vertebrates, the same spectral absorbance can be realized by opsins with quite different amino acid sequences. It seems likely that this leaves elbow room for natural selection favouring residues or combinations that specifically increase thermal stability with little or no effect on spectral absorbance. Precisely to what extent this is possible is an unresolved question of fundamental evolutionary interest, for which amphibian photoreceptors offer a great study system.

For example, the rhodopsins of bullfrog (*Lithobates catesbeianus,* formerly *Rana catesbeiana*) and two toads (*Bufo bufo* and *Rhinella marina*) have virtually identical wavelengths of maximum absorbance ($\lambda_{max} \approx 502-503$ nm), but pigment-related noise in their rods differs by more than one order of magnitude (bullfrog low, toads higher) [32]. There are other examples of similar discrepancies, but this one highlights two advantages of the anuran models. First, since the species are relatively closely related, it is possible to pin down relevant molecular differences to a few amino acid residues in the opsins [33]. Second, at least in this case, a comparison of life histories immediately suggests a specific hypothesis. Besides the usual retinal (A1) chromophore of most vertebrate rhodopsins, the bullfrog uses the 3,4-didehydroretinal (A2) chromophore not only in the tadpole stage but to a varying extent all through life [34]. The A2 chromophore red-shifts the pigment, but makes it thermally less stable [35]. The toads never use A2. Has the bullfrog opsin been selected to be especially stabilizing in order to limit the noisiness of the A2 version of the pigment (the porphyropsin), getting extreme stability of the A1 version (rhodopsin) in the bargain? This hypothesis has received some support from experiments on rods of larval tiger salamander (*Ambystoma tigrinum*). When its native chromophore A2 is exchanged for A1, the resulting A1 pigment is extremely silent, just as in the bullfrog [32,36].

Cone pigments are generically different from rod pigments. They show a similar correlation between λ_{max} and rates of thermal activations, but on a 3-log-units higher general level of noisiness [28,29]. This is thought to reflect the openness of the chromophore pocket, ensuring faster chromophore exchange and thus faster recovery of cone pigments after bleaching, and is formally encapsulated in a higher "pre-exponential factor" of Arrhenius-type equations for reaction kinetics. The work of Yoshinori Shichida and colleagues is now shedding light on the

molecular substrate of this generic difference [37,38]. An especially interesting study object is the unique amphibian rod- like receptor known as the “green rod” because it looks green in a retinal flatmount [9,39] although it contains a blue-cone pigment [40,41]. In anurans (but not in urodeles) this pigment, which belongs to “class 2” of the two classes of short-wavelength sensitive cone pigments (SWS2), has acquired rod-like stability by a single amino-acid mutation [38]. It is still controversial exactly how silent it is [29,42], but the blue- and green-sensitive rods (which we shall hereafter refer to as BS and GS rods) together do enable frogs to make behavioural blue-green colour discriminations near their absolute visual threshold, at light intensities where mammals see nothing at all [43]. Remarkably, the stabilized anuran BS-rod pigment has retained the fast regeneration kinetics of cone pigments [44]. It remains an intriguing object for investigations of the molecular underpinnings of visual-pigment properties (see further 2.3. below).

Clarifying molecular mechanisms, possibilities and limits of thermal stabilization independent of spectral properties is of fundamental interest for understanding the natural selection of visual pigments. It may also deepen insight into the universal long-wavelength (“infra-red”) limit of animal vision, generally attributed to the impossibility of making visual pigments with λ_{max} beyond the naturally occurring limit (~630 nm) without incurring intolerable thermal noise. Anuran (together with urodelan) pigments offer a rich study system for this endeavour.

2.3. Photoreceptor complements and potential colour space

Whilst the big size of anuran rod outer segments (Fig. 1) compared with those of other vertebrates [45] made them workhorses of early visual neuroscience, the variability and peculiarities of the morphological and spectral types of frog photoreceptors remained largely unexplored and underexploited. The most remarkable type is the aforementioned BS rod. Shortly after their discovery [9], W. Krause identified them in yet another eight species of frogs [46], and they ended up being regarded as a synapomorphy of amphibians [47,48]. Their visual pigment, spectral absorbance ($\lambda_{max} \approx 430$ nm) and specific morphology were thoroughly characterized in some species of *Bufo* and *Rana* [49–54], and it was realized that the BS and GS rods together might enable purely rod-based colour vision [50]. Because BS rods are unique to amphibians, research about their physiology and connectivity lacked the potential to be extrapolated to other vertebrate lineages – a tacit requirement of a popular model system – and progress in this area stalled. New interest arose as gene sequencing enabled comprehensive mapping of vertebrate opsins and it was found that the pigment of BS rods belongs to a family of cone opsins (SWS2, see 2.2. above) [40], albeit associated to a rod transducin (at least in salamanders) [41]. With the more recent discovery of a single mutation that increases the stability of the anuran BS-rod pigment [38], the body of evidence suggests how BS-rods may increase our understanding of vertebrate photoreceptor evolution. The current consensus is that cones are the ancestral photoreceptor type and rods evolved from them in incremental fashion involving several steps of replacement of protein isoforms and morphological divergence [55]. The cone-like rods of lampreys [56] point to the time frame of chordate evolutionary history when the divergence started to become meaningful, but it is unclear to which degree it proceeded independently in different vertebrate lineages. The ontogenetic development of rods happens *via* recruitment of different photoreceptor precursors in mouse and zebrafish [57]. Amphibian BS-rods appear as excellent models for studying the cone-rod transition for a number of reasons. First, anurans lie phylogenetically between two lineages that generate rods in different ways (*i.e.* fish and mammals). Second, the mixture of cone and rod protein isoforms in BS-rods, and the difference between anurans and urodeles [38,41], suggests that they provide a snapshot of one stage in a transformation that happened for the first time hundreds of million years ago. Different anuran lineages could exhibit varying degrees of advancement of the transition, and comparative work on BS-rods and their pigments in more anuran species than the few that are known so far may yield important insights. A third advantage of anurans is that BS-rods appear relatively late during ontogeny [58], when the developing individual is a free-living tadpole with completely formed and accessible eyes [59].

Besides the two rod types, anurans in general have both single and double cones [45,54] completing their typical vertebrate duplex retinas (Fig. 1). The number of spectral types remains controversial: red- sensitive cones (RS-cones) have been known for several decades and have peaks at approximately 565 nm (see [60] regarding a deviating result reported in [53]). The pigments are typical long-wavelength sensitive

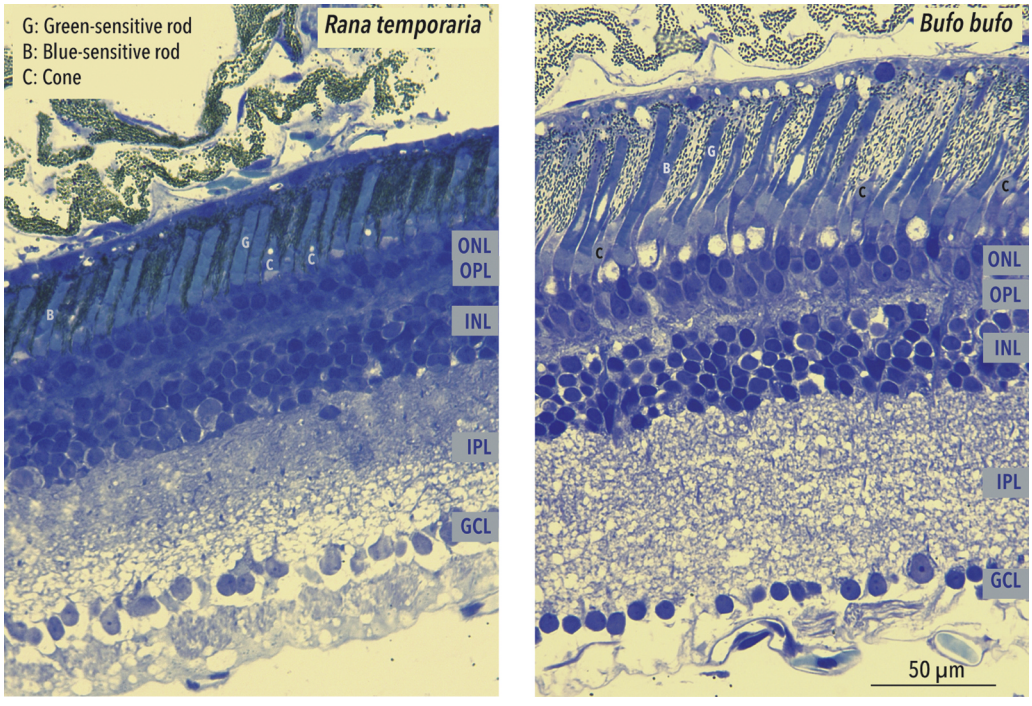

Fig. 1. Sagittal retinal sections from two anuran species commonly used in vision research, stained with Methylene Blue + Azur II. Note the oil droplets in the short, wide cones of *Rana temporaria*, and the glycogen inclusions (paraboloids) in the long, slender cones of *Bufo bufo*. ONL: Outer Nuclear Layer; OPL: Outer Plexiform Layer; INL: Inner Nuclear Layer; IPL: Inner Plexiform Layer; GCL: Ganglion Cell Layer. The photoreceptor legend and scale bar are the same for both pictures.

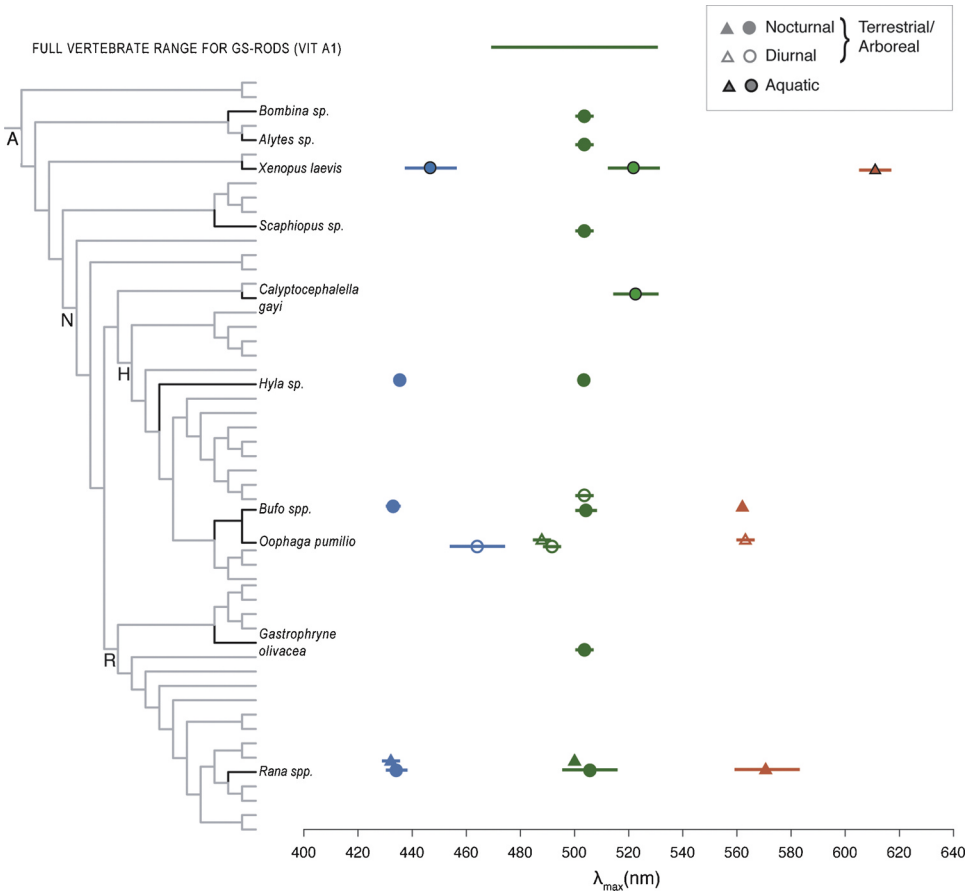

Fig. 2. Peak spectral sensitivities (λ_{max}) of adult anuran photoreceptors and/or their visual pigments (circles: rods, triangles: cones). The tree topology is from [76], and the letters in internal nodes show major taxonomic groupings for reference: A: Anura; N: Neobatrachia; H: Hyloidea; R: Ranoidea. Each terminal branch represents one of the 53 families proposed in the source, and the genera/species names point to the lineages within them for which data are available. ERG data from *Rana*, *Bufo* and *Hyla* [77–79] showing approximately the same maxima for the GS- rod dominated scotopic and RS-cone dominated photopic curves are not shown here to avoid clutter. References: *Bombina, Alytes, Scaphiopus* [71], *Gastrophryne (Microhyla) olivacea* [74,75], *Xenopus laevis* [23,62,80], *Calyptocephalella gayi (Caudiverbera caudiverbera)* [81] *Hyla* [82], *Bufo* [23,27,74,83–85] and unpublished data from S. Kondrashev reported in [43], *Oophaga (Dendrobates) pumilio* [86], *Rana* [23,52,53,60,63,80,87], general vertebrate range [88].

(LWS) pigments [61]. Blue-sensitive cones went unnoticed for a long time [53,62], with a first anecdotal mention of a "blue-absorbing visual pigment" in bullfrog cones in the early 1980s [63]. Spectral sensitivity curves ($\lambda_{max} \approx 433$ nm) were published only a decade later for its close relative *Rana temporaria* in [60], where it is further mentioned that they are present also in *R.* (*Lithobates*) *pipiens*. They seem to be the smallest and least abundant cone type (*Xenopus*: [64]). This, together with general subsampling by the microspectrophotometry (MSP) technique and the fragility of cone outer segments [53] makes it seem likely that BS-cones are common in anurans. At least in the bullfrog, BS-cones, although spectrally indistinguishable from BS-rods, carry an SWS1 opsin instead of SWS2 [65]. This finding is quite remarkable: SWS1 and SWS2 opsins, which evolved independently after the duplication of the ancestral SWS gene, normally perform a "division of labour" when both are present [66], covering the UV/violet and blue parts of the spectrum, respectively, rather than converging on virtually the same spectral absorbance. There are no reports of any anuran having SWS1 cones with sensitivity maxima in the UV, or of SWS2 cones (in contrast to urodeles [41]).

Green-sensitive cones (GS-cones) are a long standing mystery among amphibian photoreceptors. Some studies have reported that the accessory member of some double cones has a green-absorbing pigment with $\lambda_{max} \approx 500$ nm (virtually equal to GS-rods) in two species of *Lithobates* (formerly *Rana*) [53,63], although others could not identify them in other species of the same genus [60]. None of the expected opsins for a GS-cone ("rhodopsin, type 2" (Rh2) as in fish or birds, or a green-shifted duplication of LWS as in some primates) has ever been identified in amphibians [67,68], and indeed, no Rh2 gene is listed in one of the more comprehensive compilations of vertebrate visual opsin genes [66]. Furthermore, attempts to obtain cDNA clones encoding the Rh2 opsin and to immunostain cones with an anti-Rh antibody have proved unsuccessful at least in newts [69]. On the other hand, early morphological studies on *Rana temporaria* noted that the accessory member of double cones have rod-like features [70], leading to the speculation that these might actually be rods fused to single cones [71], whereby it might well contain normal rod rhodopsin. However, this hypothesis has not been followed up on, the original evidence is unclear regarding the developmental stage in which the histological observations were made, and other authors do not mention a potential rod-identity for the accessory member of the double cone [54]. Single-cell transcriptomics could aid to solve this mystery once and for all.

From the photoreceptor complements described above, it follows that photopic, cone-based colour vision in anurans could be either dichromatic (if GS-cones are absent) or trichromatic (if GS-cones are present). Mesopic colour vision combining cone and rod signals could be trichromatic. Finally, scotopic colour vision based on BS and GS rods (*i.e.*, dichromatic) is plausible in anurans as well as urodeles, in contrast to all other vertebrates. On the other hand, given that the SWS1 and SWS2 opsins found so far in anurans are spectrally indistinguishable, the potential for tetrachromatic colour vision is ruled out at the moment. Colour vision in itself has been demonstrated in several behavioural experiments in anurans during the 20th century (see [72] for a list), but none of these tested its dimensionality, or the degree to which cones or rods are involved. The more recent behavioural demonstration of purely rod-based green/blue discrimination in *Rana temporaria* [43], pushes the illumination threshold for colour vision in anurans far lower than for any other vertebrate tested [73].

2.4. Visual pigments and photoreceptors across anuran ecological and phylogenetic diversity

Photoreceptor spectral sensitivities determine both overall visual sensitivity in a particular spectral environment and the chromatic space of colour vision. The position of the spectral sensitivity peaks (λ_{max})

depends on the amino acid sequence of the opsin protein and the type of retinal (A1 or A2) used as chromophore (see 2.2. above). About anuran rods, Fred Crescitelli noted already in 1958: “The interesting feature of the amphibian rhodopsin system is its location within a very restricted region of the spectrum. This is in contrast to the [rhodopsin] pigments of fish, reptiles, and even of mammals (…). This spectral constancy of amphibian rhodopsin holds true in spite of wide variations in habitat.” [74]. Fig. 2, summarizing much of current knowledge on the spectral identities of anuran photoreceptors, shows that this observation still stands today. Admittedly, the

available sources are limited in terms of species covered, reflecting the historical importance of the genera *Bufo* and *Rana*, and it is possible that the ranges are broader than we currently know. Furthermore, a substantial part of the literature is rather obscure regarding the values and sources of the data [71,74,75] and must be taken with caution. Yet, some interesting trends can be discerned, pointing to key areas in need of further research.

First, the only two aquatic species for which there are data available – *Xenopus laevis* and *Calyptocephalella gayi* (formerly *Caudiverbera caudiverbera*) – have mostly A2-based pigments with associated absorbance shifts towards longer wavelengths ([23,62,80,81], Fig. 2). Recent estimates suggest that aquatic/semi-aquatic lifestyles throughout adulthood have evolved independently at least 11 times from terrestrial ancestors among anurans [89]. These multiple origins within the framework of relatively limited genetic distances and divergence times offer an excellent opportunity to study plasticity and convergence of the pathways involved in vitamin A metabolism and opsin spectral tuning. Most adult anurans are terrestrial and predominantly use A1 pigments, while the tadpoles of some species use A2 and A1 in varying proportions (*e.g. Lithobates pipiens* [53], *Rana temporaria* [90]) and others pure A1 (*e.g. Bufo bufo* [90]). Even in species that spend their whole life cycle in water, such as *Xenopus laevis*, there seems to be a shift from A2 towards A1 during metamorphosis [91] (but see [92]). Moreover, there is phenotypic plasticity responding to light régime and temperature in the A1/A2 ratio of *Rana spp.* [34,92–95]. These topics have been thoroughly reviewed in the 1970s [71,96]. Intriguingly, both the ratio and the timing of the switch between the two chromophores can differ between rods and cones during larval development [90]. Approximately 75 % of anuran species go through a tadpole phase, as opposed to a directly-developing minority [97], and at least 18 different ecomorphological tadpole guilds have been characterised based on microhabitat type, morphology, and behaviour [98]. Broadening the taxonomic scope in studies of tadpole pigments could illuminate development, evolution and plasticity of the vitamin A system at the aquatic-terrestrial interface, and the role that different fresh-water microhabitats play in shaping it.

As seen in Fig. 2, there is one notable exception among A1-based frog pigments from the general λ_{max} pattern, and this is the only unequivocally diurnal species in the Figure, *Oophaga* (formerly *Dendrobates*) *pumilio* [86]. All the photoreceptors of this frog differ from the standard picture outlined so far (except the RS-cone peaking at the usual 562 – 564 nm). First, the BS-rods seem to be absent in this species, an undoubtedly suggestive finding for a diurnal species. Second, the GS-rods have a short-wavelength shifted peak, close to 490 nm, which so far is the only known significant departure from the 500 – 503 nm “standard”. Third, this species possesses the controversial GS-cones with spectral sensitivity closely matching that of the GS-rods, but in this case, too, the identity of the opsin is unknown (see 2.3. above). Fourth, it also possesses BS-cones, but with rather variable λ_{max} (range 457 – 471 nm). This suggests a remarkable long-wavelength shift of the presumed SWS1 pigment, and might also indicate co-expression of two or several visual pigments, as known from salamander cones [99,100]. Together with the apparent absence of BS-rods and the unusually stringent removal of UV and violet/blue light by the lens (see Table 1 and 2.5. below), this shows a remarkable co-adaptation of basic eye parameters. Modelling of a trichromatic colour space has showed that

Table 1
Summary of data available for selected features of the visual system in some anuran lineages (adults only).

Habitat, Diel pattern	Species	Rod:Cone ratio	Rod outer segment (µm)		Optical sensitivity	Cone oil droplets	Lens λ_{T50} (nm)
			Length	Diameter			
Semi-aquatic, Diurnal/Nocturnal	*Bombina spp.*	N/D		6.5 (1) [104]	N/D	No (2) [104]	280 (1) [105]
Aquatic, Arrhythmic	*Xenopus laevis*	53:47 [64]	45 [64]	7 [64]	N/D	Yes [64,104]	N/D
Arboreal, Nocturnal	*“Hyla” spp.*	N/D	43 (1) [106]	5.2 – 7.8 (7) [104,106]	15 – 18 (1) [106]	No (16) [104]	392 – 399 (4) [105]
Terrestrial, Nocturnal	*“Bufo” spp.*	71:29 (1) [107]	45 – 68 (2) [26,84,85,107]	7.3 – 8 (2) [26,84,104,107]	20 – 29 (2) [102](*)	No (16) [104]	341 – 361 (3) [105,108]
Semi-aquatic/Terrestrial Arrhythmic/Nocturnal	*“Rana” spp.*	65:35 (1) [54]	27 – 55 (1) [53,54,106,112]	5 – 8 (8) [53,54,104,106,112]	14 – 18 (1) [106]	Yes (12) No (1) [104,109]	396 – 403 (3) [105,108,110,111]
Terrestrial, Diurnal	*Oophaga pumilio*	N/D	19 [106]	3 [106]	1 [106]	Yes [86,104]	425 [105]
Terrestrial, Diurnal	*Mantella viridis*	N/D	32 [106]	6 [106]	7.4 [106]	N/D	N/D

Information and classification criteria for habitat and diel pattern are from [89] and [101], respectively. Values in parentheses indicate the number of species covered by the cited literature. Optical sensitivities have been calculated according to [102]. The value given in [102] for *“Bufo”* spp. (*) is ten times lower than here, but it is based on an outer segment diameter (2.5 µm) that is improbably small for toad rods and not even given in the source of the data (from *Bufo americanus*) [103]. The range given here has been calculated using the dimensions of *Rhinella marina* [85] and *Bufo bufo* [26] rods. N/D: No data available. Data on oil droplets and rod diameter exists for 97 species in total [104], and on lens transmittance for 37 [105].

the three cone types of *Oophaga* can support colour-based detection of conspecifics against the background in this highly colour-polymorphic species [86], but does not help to explain the spectral shifts of BS- and GS-cones, and in opposite directions, compared with other frogs. The vast majority of anurans are nocturnal, but diurnality has evolved independently several times [101]. This single example of one diurnal species, *Oophaga pumilio*, highlights how much there is to learn by looking beyond the *Bufo-Rana* axis.

2.5. Optical and anatomical constraints to photoreceptor performance and spectral sensitivity

Besides photoreceptor spectral sensitivities, there are a number of other eye properties that influence how well a visual system can perform in different environments. A summary of available data about some of those key aspects is shown in Table 1. There are gaps even in the most popular study species, *e.g. Xenopus laevis*, as well as others that have been reasonably frequently used in vision research, such as *Hyla spp.* and *Bombina spp.* More strikingly, it shows how underexplored the anuran diversity is in terms of even the most basic features, such as the relative proportions of rods and cones. Anuran retinas are rod-dominated in the few species for which we have data, consistent with the nocturnal ancestry of the lineage and lifestyle of the majority of its extant representatives [101]. However, there is no information on rod:cone ratios in diurnal species, which makes it impossible to judge to what degree these depend on the lifestyle and the time of divergence from the nocturnal ancestor.

The light sensitivity of the whole eye under different illumination conditions depends not only on the number and gain of photoreceptors that are operational in each situation, but also on the light- collecting properties (the "optical sensitivity") of each individual photoreceptor type. This property is influenced by the dimensions of the photosensitive portion of the cell (the outer segment), by possible light-collecting structures in front of the outer segment, by the pupillary aperture that regulates the amount of incoming light, and by the focal distance of the eye, which determines the acceptance angle of the stimulus [102,113]. Recently, a study where diurnal and nocturnal frogs were compared for the first time [106] reported that rod optical sensitivities in diurnal species, albeit variable, are significantly lower than those of nocturnal species (Table 1), and showed that this correlated with lower scotopic sensitivity as recorded by ERG. The same study also reported, for the first time, rod outer segment dimensions for any diurnal anuran (significantly smaller than in their nocturnal relatives, Table 1). A decrease in collecting area of the dim-light photoreceptor is probably no great loss for a diurnal species, and might suggest a trade-off in favour of cones, possibly translating into improved photopic sensitivity and/or spatial resolution. Indeed, the photopic (cone-driven) ERG showed higher sensitivity in the diurnal compared with the nocturnal species [106]. These pilot results again remind us of the need of diversification in the choice of study species to unveil evolutionary patterns between (and within) diurnal and nocturnal lineages and to illuminate their visual ecology.

No amphibian species has been found to possess coloured oil droplets in cones (as is common in birds and reptiles), but many species have transparent oil droplets in some single cones and in the principal member of the double cone ([45,104], Table 1, Fig. 1). There is no obvious correlation with the ecology of the species, and the evolutionary trajectories of acquisitions/losses are unknown. Colourless oil droplets increase the photon catch of cones, as specifically shown for *Xenopus laevis*, while coloured oil droplets decrease it [114]. So far, all oil-droplet-bearing frog cones (whether singles or principal members of doubles) have been identified as red-sensitive [53,64,86] and they are also the ones with the biggest outer segments [64]. Enhancing light capture with oil droplets will increase the sensitivity of the RS-cones, which is likely to increase the dynamic range for colour vision based on comparison of RS- and BS-mediated responses: RS-cones are noisier and have lower gain than BS-cones [115], which, other things being equal, means that in a certain dim-light range BS cones are still active, but there is no RS-signal to compare with. Indeed, behavioural experiments on colour discrimination in *Bufo*, a genus that lacks oil droplets, have shown that colour discrimination based on differences in the "red" channel is lost already at much higher light levels than discrimination based on differences in the "blue" channel [43]. Oil droplets could partly compensate for the difference, improving the match between BS and RS operating ranges and thus extending cone-based colour vision to lower illuminations. This might explain the ubiquity of oil droplets among frogs, where many species classified as "nocturnal" are still active in a wide range of crepuscular conditions [101].

Finally, the absorbance properties of the ocular media (cornea, lens and humours) affect the performance of the visual system by filtering light before it reaches the retina. Light in the UV and violet-blue range is eliminated, presumably because it is potentially harmful and is optically problematic due to scattering and chromatic aberration. Vertebrate eyes in general, including those of the majority of the anurans that have been studied, transmit more short wavelengths than the human eye [105]. The cut-off wavelengths where lens transmittance has fallen to 50 % of maximum (λ_{T50}) are given in Table 1 for those of the listed species where it is available. There can be ~ 50 nm differences in λ_{T50} between species that share the same spatial and temporal habitats, *e.g.*, *Bufo bufo* and *Rana temporaria* [108]. Most interestingly, however, some diurnal species filter out all the UV and part of the violet/blue light similarly to humans, up to 425 nm [105]. One of these is *Oophaga pumilio* (Table 1), whose exceptionally long-wavelength shifted BS-cones were discussed in the previous section. The shift makes sense: while the lens applies a strict limit to the UV and violet light that is richly present in sunlight, BS-cone absorbance has moved into a range that is not much attenuated (see [108] for examples of superposition between lens and photoreceptor spectral absorbances). Again, it is clear that "standard" frog spectral sensitivities cannot be assumed to apply universally.

3. Retinal ganglion cells and visually-guided behaviour

3.1. Sensitivity and coding of intensity and colour

In the last years of the 1930's, the frog retina yielded the first single-cell spike recordings from the retina of any species, as Keffer Hartline [116] isolated single ganglion-cell (GC) axons by microdissection, and Ragnar Granit (together with Gunnar Svaetichin) [117,118] sampled single "spiking units" in the intact retinal tissue with a novel microelectrode. The work of these Nobel laureates was ground-breaking for understanding spatial organization and coding of intensity and colour in vertebrate retinas. In their wake, Horace Barlow [119] described lateral inhibition and the center-surround organization of the receptive fields (RFs) of frog GCs simultaneously with Stephen Kuffler's [120] work on cat. Through the following decades, anurans remained important in retinal research based on extracellular spike recordings facing two ways: on one hand, information encoding by GC spike discharges (including their tectal and thalamic projections), on the other hand, aspects of intraretinal information processing and adaptation that shape the spike discharges.

Special advantages of anuran GCs are the precision afforded by generally silent cells signalling with few spikes or distinct bursts of high significance, and the relative ease of obtaining stable and long- lasting (> 10 h) recordings from the eyecup. This was crucial for experiments on GC dark adaptation, which in the 1960s (when correlated with the kinetics of pigment bleaching products in extracts) mounted a challenge to the then dominant Dowling-Rushton paradigm, where all retinal adaptation not connected with bleaching of substantial fractions of pigment was attributed to "the neural network" [121,122]. Somewhat paradoxically, spike recordings at the retinal output in frogs helped to put the gain controls of vertebrate photoreceptors back into the picture

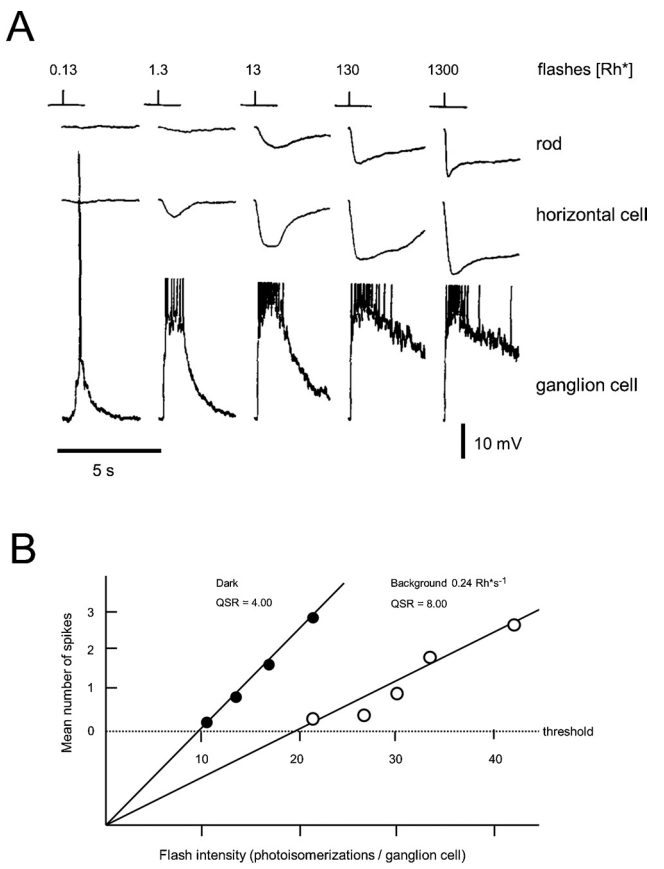

Fig. 3. Signal transfer and ganglion cell output in anuran retina.
A. Increase of response amplitude over three processing levels in the dark-adapted retina of the cane toad (*Rhinella marina*): intracellularly recorded voltage responses of a rod, a horizontal cell and a spiking cell (presumed GC) to the same five flash intensities, as shown in the top row in terms of isomerizations per rod [Rh*] (spot diameter 0.75 mm on the retina, 13.5 ms flashes). The scale bars for time (5 s) and response amplitude (10 mV) hold for all responses. In the spiking responses, the full amplitude of the action potential is shown only in the first column; in the others, the spikes have been truncated for clarity. Note that at the GC spiking threshold, no response can be seen in a single rod. Temperature 20 °C. After [150].
B. Linearity of quantum/spike encoding in a frog GC (*Rana temporaria*) in darkness (solid circles) and under a dim background light (open circles). Each data point shows the mean number of spikes in extracellularly recorded responses to 12 presentations of nominally the same 67 ms flash. The background delivered 0.24 isomerizations per rod per second [0.24 Rh*s-1], chosen to double the flash intensity needed to elicit a spiking response on 50 % of the trials. Flash intensity is given on the abscissa as numbers of isomerizations in the receptive field (RF) of the GC. The RF encompassed 230 rods, thus the value 10 corresponds to ca. 0.04 Rh*, *i.e.* 3 times less than the dimmest flash in panel A. Due to the small RF and the low temperature of the experiment (11.5 °C) the predicted rate of rod dark events affecting the GC is only about 1.6 events per integration time, and indeed the cell acts almost as a noise-free photon counter, in darkness giving one spike for every 4 photoisomerizations above threshold. The straight line fitted to the solid symbols but constrained to go through the origin shows a quantum/spike ratio QSR = 4 above threshold. The background that doubled threshold intensity also doubled the QSR (the line fitted to the open symbols shows QSR = 8), indicating that linearity is preserved and the physiological thresholding nonlinearity is unaltered, but the retinal gain prior to spike generation is decreased by half.

(reviewed in [123]).

The "cybernetic" approach to frog GCs in the 1960's (see Section 3.2 below) attracted the attention of the entire neuroscience community, but accelerated the divergence of mammalian and amphibian research. However, the crisp messages of the frog and toad retinal output cells continued to enable discovery of several general mechanisms, some of which are enumerated below:

(i) Multiplexing of on-off, luminosity and chromatic contrast information by single GCs through distinct temporal response patterns [124–128]. Colour-coding in the light-adapted anuran retina relies on opponency of a long-latency "surround" pathway getting input from blue-sensitive receptors, against a red-cone-mediated "centre" pathway (*Rana temporaria, Bufo bufo*) [129–131]. The original attribution of the blue-sensitive responses to BS rods based on experiments using strong GS-rod-suppressing background light must be questioned, however, especially as blue cones were unknown at the time. The question remains unresolved: a "surround" input from BS rods is suggested by an EM and electrophysiological study of *Lithobates pipiens* showing that "giant" outer horizontal cells contact BS rods and get blue-sensitive input of opposite sign to the red-cone input [132]. On the other hand no input from BS rods has been found in *Xenopus* horizontal cells [133]. The identity of the blue input in different states of adaptation is of considerable interest, because the phototactic response of frogs to "blueness" is opposite in photopic and scotopic conditions [43].

(ii) Adaptation of GCs to light fluctuations, attenuating responses to temporal contrast and returning the maintained discharge to a low basal level during prolonged exposure of the RF or its subunits to temporal changes of low information value [134]. Similar effects have later been found and carefully modelled in salamander and rabbit retinas [135]. In anurans, it might reflect the same proximal mechanism that implements "noise adaptation" [136], which elevates the threshold intensity of GCs in proportion to the quantal fluctuations of dim backgrounds. The functional outcome of the latter is that spikes signal light excursions of constant statistical significance.

(iii) Seasonal changes in retinal function. In *Bufo bufo*, the response properties of specific GC classes were found to change, partly correlating with changes in contrast preference of the prey- catching behaviour [137]. Seasonal changes in the properties of *Rana temporaria* GCs, especially increases in the maintained activity of off cells in spring, have been observed also by one of the present authors (unpublished). The underlying mechanisms are unknown, and this is a field that would merit further investigation.

(iv) Spatial asymmetry of the inhibitory RF-surround, which confers one form of selectivity for direction of movement [138,139].

By contrast, anurans with their complex retinal network and relatively small neurons played no major role in pioneer studies unravelling retinal circuitry by intracellular voltage recording. The animal of choice was the urodele *Necturus maculosus* with its big neurons and simple visual system [140]. Characteristically, only 9 out of 69 references in John Dowling's 1976 review in the book Frog Neurobiology, "Physiology and morphology of the retina" [141], explicitly concern frogs or toads. In his previous EM study of the frog retina [142] he had expressed doubts "…that one could ever understand the complex synaptic interactions occurring among the amacrine cell processes … by single-unit recording from any one of the cells. It is questionable whether even multiple-cell recordings could yield this information." In the framework of classical electrophysiology, this probably remains true, but the prospects look very different given the methodological arsenal available today (see *e.g* [143].). Even in the late 1970's, pharmacological experiments allowed some insight into amacrine circuitry shaping GC response patterns, especially on the role of GABAergic and glycinergic inhibitory interactions [126,138,144]. One of the GC effects described (in *Rana temporaria*) was that the rhythmicity of responses of off-cells ("dimming detectors") was abolished by the glycine antagonist strychnine [144]. Off-cell oscillations attracted new interest in a perceptual-binding context around the turn of the millennium. Masao Tachibana and colleagues [145–147] found (in *Lithobates catesbeianus*) that oscillations were synchronized across large parts of the retina, and that the oscillations, but not the spike responses to dimming as such, were suppressed by the GABAA antagonist bicuculline (with little effect of strychnine). The truly interesting observation was that bicuculline also abolished the escape behaviour that is normally associated with

activity of these cells, supposed to alert against looming predators.

As a counterpoint to the daunting complexity of the amacrine-cell network and the "feature- detecting" approach to GCs (see 3.2. below), we should also like to emphasize the suitability of anuran retina for quantitative measurements by simple flash/step stimulation protocols, especially near the absolute visual threshold. In the 1980's, David Copenhagen and colleagues performed a series of fundamental studies on the transmission of voltage signals and noise through the dark- adapted retina of the cane toad (*Rhinella marina*) [136,148–150], backed by the knowledge of rod responses and dark noise provided by suction-pipette current recordings in the same species [20,24]. Increases in the amplitude and signal-to-noise ratio of small flash responses upon passing to second- and third-order neurons were consistent with predictions based on linear summation of rod signals within their RFs (Fig. 3A). The results illuminate the different strategies for handling signal/noise in amphibian and mammalian retina. Spatial averaging takes place already in the electrically coupled rod network [21], and so anurans allow the first synapse to work linearly, since a photon response in one rod is not confined to that rod. Instead, it is present as a low-amplitude common-mode deflection in tens of rod synapses (undetectable in a single rod; see the leftmost rod recording in Fig. 3A), to be reassembled and amplified in higher-order neurons (here, horizontal and GC).

Anurans then apply a high threshold at the GC level, preceded by a synaptic "noise gain box" [136]. This leads to rejection of most noise before spike generation, yet retaining the linear scaling of (small) supra-threshold signals in the GC output (Fig. 3B, from *Rana temporaria*). By contrast, mice perform stringent thresholding to discriminate photon signals from continuous noise in each rod-to-rodbipolar synapse, sacrificing an astonishing fraction of all single-photon responses in the process (see [151]).

3.2. What the frog's eye tells the frog's brain

In 1948, Norbert Wiener at MIT published "Cybernetics: or Control and Communication in the Animal and the Machine" [152], establishing the new science of cybernetics. Jerry Lettvin and two other prominent members of Wiener's circle (Warren McCulloch and Walter Pitts), together with the young Chilean neuroanatomist Humberto Maturana then in Boston [4,5], made frogs and toads the cherished models of a remarkable endeavour where cybernetics cross-bred with a new branch of ethology called neuroethology (*e.g* [153].). The frog's retina became the paradigm of a "smart" retina, with (at least) five specialized GC classes filtering and parsimoniously encoding specific features of visual scenes. The reality of the classes was substantiated by their distinct morphologies and terminal layering in the tectum. They were listed as (1) sustained edge detectors, (2) net convexity detectors, (3) moving-edge detectors, (4) net-dimming detectors and (5) dark detectors. What caught popular imagination was the suggestion that class 2 could serve as "bug perceivers", echoing Barlow's earlier consideration [119] of a type of on-off center cell with inhibitory RF surround as a "fly detector".

The feature-detector view immediately suggested the hypothesis that there might be rapid one-to-one coupling of responses of a specific GC class to a standardized behavioural response ("fixed action pattern" in ethological terminology): snapping after small moving "prey" (class 2), or escaping a predator causing dimming of the RF (class 4). However, systematic investigations [154,155] showed that none of the Lettvin-Maturana-type stimuli would activate only a single class of GCs. Conversely, no toad neurons were found that would respond specifically to a supposed key stimulus such as a moving, worm-like object [156]. The simple hypothesis that a single type of GC could as such represent a key-stimulus-specific "innate release mechanism" in the sense of Konrad Lorenz [157] had to be reformulated in terms of flexible weighing of inputs from parallel matched filters [154,158].

The ethological focus of frog research meant that it diverged from the mammalian mainstream (or maybe vice versa). In mammals, feature extraction was relegated to the visual cortex, and retinal GCs were classified by general dichotomies: on/off, linear/non-linear, sustained/transient, brisk/sluggish, X (β) / Y (α), midget/parasol, parvo/magno. Yet, mammalian retinal research ultimately had to address the function of "excessive" numbers of GC classes (based on a combination of functional, morphological and genetic criteria by now amounting to > 20 in primates and twice as many in mouse, [159]). In their influential 2010 article "Eye smarter than scientists believed: neural computations in circuits of the retina", Tim Gollisch and Markus Meister [160] reinvented the mouse as a mammalian frog. They noted that "many of the examples quoted here are from 'lower' vertebrates, meaning nonprimates" and argued for human relevance by referring to the similar anatomical complexity of primate and mouse retina. The frog remained conspicuously absent.

With few exceptions, the field of frog GC research has been little cultivated for 20 years. Now might be the time to learn from mouse and return to frog GCs with the full battery of state-of-the-art imaging and electrophysiology and optogenetic interventions. Already in 1894, Ramón y Cajal distinguished 11 morphological subtypes of frog ganglion cells [161], and while two histological studies from the 1980's [162,163] discerned only 7 and 5, respectively, both found one type not detected by the other. Rare types easily escape detection, and the resolution of types by classical histology is limited anyway: "There is variation within these physiological and histological groups, and much room for still unidentified subclasses" [163]. Electrophysiological studies have reported several functional types that do not fit into the Lettvin-Maturana scheme (*e.g* [126,130,164].). In a comparative perspective, full mapping of frog GCs by modern methods could contribute much to the understanding of universal tetrapod principles. In an ecological perspective, it could liberate the study and interpretation of frog behaviour in natural environments from the confines of the 5 canonical classes. The easily accessed tectum and thalamus also appear as attractive targets for optical recording in freely moving frogs.

3.3. Ganglion cell topography, visual acuity and visual signalling

Besides the feature-encoding properties of different GC classes, their retinal densities and regional distribution determines what can be detected in different parts of the visual field. Anurans apparently lack foveas but can have more subtle regional specializations such as areae centralis and visual streaks (see [165] for a comprehensive discussion). Anatomical estimates of visual resolving power based on eye focal length and GC densities [113] are scarce. Information from four nocturnal species (*Lithobates pipiens*, *Hyla japonica*, *Hyla raniceps* and *Bombina bombina*) suggests 2.7–6.3 cycles/deg of maximum resolving power [165–168], which is relatively low among vertebrates [169]. This may be expected, as frog eyes, although big in relative terms, are rather small in absolute terms, which sets a limits on focal distance. The potential spatial resolving power has not been calculated for any diurnal frog species. Under any circumstances, resolution is task-dependent, and the common measure, based on the assumption of linear transfer of contrast modulated gratings by a generalized cell mosaic, can be no more than suggestive. In reality, independent sub-mosaics are formed by the different cell classes, each with its own characteristics for detection and localization of events in space and time [4,5] (see below).

The function of colour in anurans is probably not to support discrimination of fine details, but to work as a signal *per se* at a coarser spatial scale. Whole-body colouration is crucially important for sex-discrimination and mate choice in some species [43,169]. Thus male *Rana temporaria* (bluish themselves) may even be more attracted by a bright red ping pong ball dragged across the surface of the breeding pond than by real (reddish) females [170]. Male moor frogs (*Rana arvalis wolterstorffi*) develop a conspicuous dorsal blue-UV colouration during the breeding season, hypothesized to act both as a fitness signal and against male-male coupling [171]. In mate choice experiments with *Bufo bufo*, males prefer bluish targets and have been found to exhibit

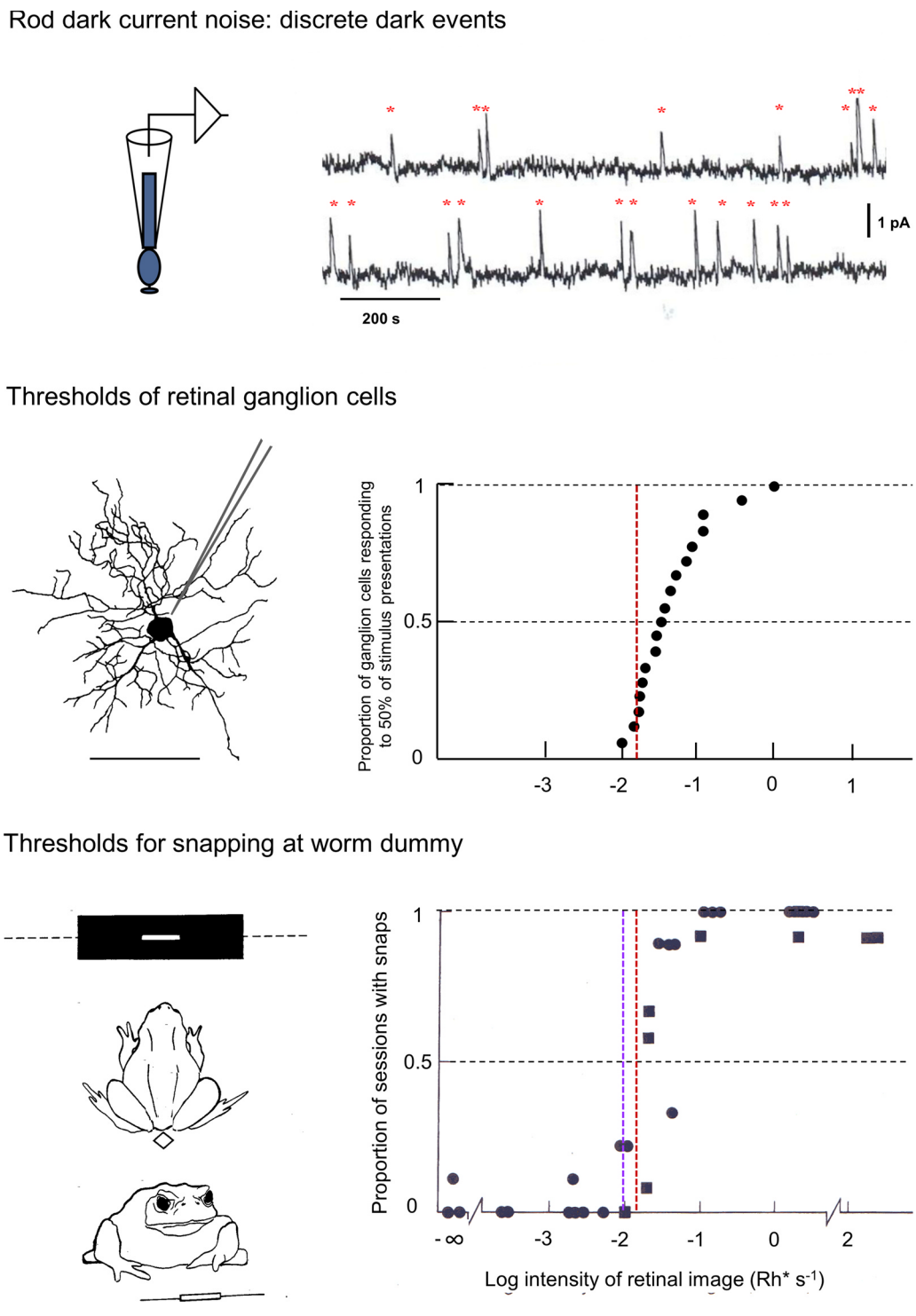

Fig. 4. Comparing the performance of rods, ganglion cells and behaviour near the absolute visual threshold, all in the same species, *Bufo bufo*. Correlation of the absolute visual sensitivity measured by the prey-catching behaviour, the rate of randomly occurring discrete dark events in rods, and the sensitivity of dark-adapted retinal GCs.

Top panel: The outer-segment current of a rod recorded in darkness by the suction-pipette technique (configuration shown on the left). In ca. 40 min of recording, 21 discrete isomerization-like events can be counted by eye (marked by red stars), suggesting a dark event rate of ~0.01 Rh*s-1. A larger material and analysis indicated a mean value of ~0.015 Rh*s-1 at the temperature of the recording, 16 °C. This dark event rate is marked in the other panels as a red dashed line. After [202].

Middle panel: The distribution of extracellularly recorded spiking thresholds of 18 dark-adapted GCs in the dark-adapted *Bufo bufo* retina. Each data point shows, for one on/off cell, the log stimulus intensity [Rh*s-1] needed to elicit at least one spike on 50 % of the trials. The stimulus was a rectangle mimicking the retinal image of the white worm dummy used in the behavioural experiment. Thresholds were the same regardless of whether the image was moved at "dummy- speed" over the RF, or presented as an on-step of light. The data points have been plotted in order of increasing threshold at equal distances on the ordinate, forming a cumulative graph showing the fraction of cells responding at each intensity. Temperature ~15 °C. After [25]. The vignette on the left imagines how an extracellular electrode is approaching a typical anuran class 3 cell (on-off cell), as seen in a Golgi-stained flat-mount (this cell, reproduced from [163], is from *Rana temporaria*, though). Horizontal scale bar 100 µm.

Bottom panel: The behavioural experiment. A toad was placed in a black plastic box with an antireflex glass window in the floor, under which white plastic worm-like dummies (3 × 20 mm) moved at constant speed (13 mm s^{-1}, one each 7.7 s) against a black background. There was no other light than a dim, carefully shielded and adjustable 525 nm light source diffusely illuminating the stage from above. If the toad saw the worm, it responded by an audible snap of the tongue against the floor. Each data point refers to a set of sessions with 12 toads, and shows the proportion of sessions during which at least one snap occurred within 2 min. Intensities are calculated in terms of photoisomerizations per rod and second [Rh*s^{-1}] produced by the image of the dummy on the retina. The proportion of sessions with snaps is seen to rise steeply just above log intensity -2, correlating closely with the threshold intensity for the most sensitive ganglion cells (mauve dashed line) and the rate of dark events in rods (red dashed line). Temperature 15 – 17 °C. After [26].

colour constancy in this choice [172].

The possible role of fluorescence as a cue involved in intraspecific recognition has recently attracted much interest. So far, it has been shown in only one species (*Boana,* formerly *Hypsiboas, punctata*) that fluorescence adds significantly to the light reflected from the body surface in natural illumination [173]. Several other species fluoresce under artificial strong UV/blue illumination [173–176], but the criteria for ecological relevance [177] have not been tested in any case, and generally the added contribution of fluorescence to the reflected light is very small in natural conditions.

For prey-catching, which relies on detection of small moving objects within a tongue-snap's distance, the spatial resolution of known GCs is quite adequate [4,5,119]. Under nocturnal conditions, the high sensitivity provided by extensive spatial and temporal summation is (up to a

limit) more relevant than spatio-temporal acuity ([26,178,179], cf. 3.4. and Fig. 3 below). However, estimating the ranges over which known behavioural displays of some species [180,181] may be effective, or the importance of colour or brightness of specific body parts in mate choice [182–185], would require data on retinal resolving power that is presently lacking. For example, at what distances can waving an arm *versus* jumping/moving the whole body be perceived? In view of the limitations on eye size, the most likely option for improving spatial resolution is increasing GC density. Topography mappings in retinal whole-mounts of species that use visual displays would enable a much better understanding of the ecological relevance of visual signals and the tasks that different parts of the visual field can support (see [186] for a recent review on the topic). In a longer perspective, large-scale optical approaches that are already being applied to zebrafish [187] for studying the retinal distribution of feature coding properties under naturalistic, ecologically relevant stimuli might be adaptable for the same purpose to (small) anurans (*e.g.* juveniles or even unusual models such as the 7-mm microhylid *Paedophryne*). Likewise, the complexities of the frog neurocircuitry would deserve to be addressed by modern electrophysiology, such as patch-clamp recording from small groups of GCs, or large-scale multi-electrode recording used for uncovering connectivity in mammals [188].

3.4. Frogs and toads as integrative research models

Behaviour provides the gold standard for functionally oriented neuroscientific research. Anurans offer exceptional possibilities for probing the visual system at crucial levels from the receptor input *via* the retinal output to behavioural decisions. They display a number of innate reactions potentially useful for experimental studies, as listed in [155]. In practice, five true visually guided behaviours have been especially useful: the optomotoric response, phototaxis, prey-catching, escape and hiding, and (for studying colour vision) mate choice. Otto Grüsser and Ursula Grüsser-Cornehls [155] have reviewed the impressive body of neuroethological work done up to the mid-1970's, largely on toads, aiming to correlate behaviour with the activity of specific GC classes according to the Lettvin-Maturana typology. This includes studies of GC responses to self-movement, lid closure and bulbus retraction, and involves recordings in the tectum of freely moving animals with electrodes controlled by micromanipulators fixed to the skull [189,190], as well as studies of behavioural reactions to stimulation of tectal and thalamic neurons through such electrodes (see [191]).

The behaviours can be harnessed in different ways to quantitative measurement of the performance limits of basic visual functions (such as sensitivity to and resolution of spatial, temporal and chromatic contrast). The spontaneous drive to approach a light source when confined in a dark environment (phototaxis) is a powerful tool that has been used to test intensity and colour preferences in more than 100 frog species [43,192–198]. Being present also in tadpoles, it can be used for studying the maturation of the visual system [199,200]. It has been used for determination of the absolute visual threshold in *Rana temporaria* and *Lithobates pipiens* [112], and for determination of the threshold for green-blue colour discrimination in the former species [43].

The first quantitative measurement of frog visual performance using a behavioural paradigm was G. Birukow's 1937 study of the optomotoric response of *R. temporaria* in a striped rotating drum, aiming to determine spatial resolution [201]. Stripes (gratings) moving behind a "worm-shaped" aperture have later been employed for the same purpose in experiments utilizing the prey-catching behaviour of *Lithobates pipiens* [168]. The lower resolution limit (2.8 vs. 4.3 cycles/deg) in [168] compared with [201] is a reminder that everything – species, geometry, and different uses of information for different behaviours – may affect results. A striking example is the finding that for prey selection (at least in laboratory conditions) *Bufo bufo* uses colour but not brightness cues, *Rana temporaria* brightness but not colour cues [43].

Fig. 4 illustrates what can be achieved by a multi-level approach in a single species (*Bufo bufo*). The aim was to localize mechanisms that limit absolute visual sensitivity, which was measured by the prey-catching behaviour. The hypothesis was that noise from randomly occurring thermal activations of rhodopsin is the factor that sets an ultimate limit for the weakest light level where the toad can still use vision (cf. 2.1. above). The rate of discrete noise events attributable to rhodopsin activations was measured by the suction-pipette technique in *Bufo* rods [202]. The sensitivity distribution of single on-off GCs in the retina was determined with a "worm stimulus". The proportion of behavioural sessions where toads responded to such moving worm dummies by snapping was determined as a function of illumination. The light level where snapping frequency started rising significantly from zero, indicating that the worm was seen, coincided closely with the thresholds of the most sensitive GCs, suggesting that the sensitivity limitation resides in the retina. The most sensitive GCs, in turn, were found to operate close to the limit set by rod dark noise events (middle panel), suggesting that these events indeed constituted an ultimate limiting factor. It may be added that this behavioural experiment, which worked so well with the toad *Bufo bufo*, could not be done with the cane toad *Rhinella marina*, because it lost interest after even a single resultless snap against the glass floor.

These behavioural experiments can be video-recorded under infrared light, which allows determination of the spatio-temporal precision of snapping. Such experiments performed under a series of dim backgrounds, at different temperatures, and with varying worm velocities and sizes have provided several fundamental insights. Snapping precision is mechanistically limited by the light-intensity-dependent latency of the retinal GCs [203], but is supported by a predictive component evident when GC latencies become long compared with worm velocity [26]. GC latencies, in turn, are long at low illumination levels, because they are determined by the slow response kinetics of the rods, which on the other hand gives the advantage of extensive temporal integration. Thus rod responses determine the trade-off between sensitivity (long integration time) and temporal precision (short reaction time) of the snapping behaviour near the absolute seeing threshold [179,203].

4. Conclusions

The deep history of vision research demonstrates the versatility and usefulness of frogs as models. This beautiful group with large eyes, a complex retina, an accessible brain, and vision as the primary sensory modality is just waiting to be rediscovered as a research model. In recent neuroscience research with state-of-the art electrophysiology, imaging technologies and optogenetics, anurans have been sadly neglected for no better reason than the fact that mice are genetically closer to humans. Moreover, the great ecological diversity of this phylogenetically restricted group sharing many fundamental constraints makes it appear as an underexploited core facility for comparative research.

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